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Anthropogenic disruptions to longstanding patterns of trophic-size structure in vertebrates

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30 **Abstract**

31 Diet and body mass are inextricably linked in vertebrates: while herbivores and carnivores have
32 converged on much larger sizes, invertivores and omnivores are, on average, much smaller,
33 leading to a roughly “U-shaped” relationship between body size and trophic guild. Although this
34 U-shaped trophic-size structure is well-documented in extant terrestrial mammals, whether this
35 pattern manifests across diverse vertebrate clades and biomes is unknown. Moreover, the
36 emergence of the U-shape over geological time and future persistence are unknown. Here we
37 compile a comprehensive dataset of diet and body size spanning several vertebrate classes and
38 show that the U-shaped pattern is taxonomically and biogeographically universal in modern
39 vertebrate groups, except for marine mammals and sea birds. We further find that, for terrestrial
40 mammals, this U-shape emerged by the Paleocene and has thus persisted for at least 66 million
41 years. Yet disruption of this fundamental trophic-size structure in mammals appears likely in the
42 next century, based on projected extinctions. Actions to prevent declines in the largest animals
43 will sustain the functioning of Earth’s wild ecosystems and biomass-energy distributions that
44 have persisted through deep time.

45 **Main text**

46 Both the ecology and evolution of organisms are substantially shaped by diet and body size.
47 Diet constrains the energy that is available for essential processes, such as metabolism and
48 growth. At the same time, body size constrains the types and volumes of food that can be
49 obtained, can be processed, and are required to survive¹. Together, these two sets of constraints
50 define the classical conception of the ecological “niche” and form the basis of much of modern
51 ecology (Fig. 1 and Extended Data Table 1). Diet and body size are therefore inextricably linked
52 across scales, from across an individual’s lifespan to macroevolutionary timescales². Previous
53 studies including different trophic guilds highlight a fundamental trophic-size structure for
54 modern terrestrial mammals, in which invertivores are limited almost exclusively to very small
55 sizes, omnivores occupy small to medium sizes, and only specialist carnivores and herbivores
56 attain the largest sizes²⁻⁴. We find that the highest and lowest trophic levels (herbivores and
57 carnivores) have greater median and maximum body sizes than the intermediate trophic levels
58 (omnivores and invertivores), leading to a relationship that is roughly “U” shaped when trophic
59 guilds are ordered along a plant to protein dietary gradient (Fig. 1, see Methods). Past literature
60 has sometimes referred to and figured this relationship as “V-shaped” (e.g.,³). While this
61 relationship is not always symmetrical and depends on the order of trophic guilds applied here,
62 for the sake of clarity, brevity, and visualization we will refer to this trophic-body size
63 relationship as “U-shaped” throughout the text.

64 This U-shaped relationship between body size and trophic status can be explained by
65 multiple physiological constraints and mechanisms (summarized in Fig. 1 and Extended Data
66 Table 1). For example, as nutrient concentrations in tissues accumulate with increasing trophic
67 level (from primary producers to carnivores), herbivores must contend with a generally nutrient-
68 poor diet⁵. Thus, herbivores tend to be large to both: a) allow for increased foraging over a wider

69 home range to maximize the amount of food consumed and b) accommodate long and/or
70 complex digestive systems that can maximize nutrient extraction (the ‘Jarman-Bell’ principle;
71 see ⁶⁻⁸). Consequently, carnivores must be large enough to traverse the same ranges as their prey
72 and also to take-down these larger-bodied herbivores (the ‘Red Queen’ hypothesis; see ^{9,10}). By
73 contrast, invertivores achieve much smaller sizes by specializing on small protein-rich
74 invertebrates whose abundance, distribution, and energy content are insufficient to support larger
75 body masses¹⁰. In comparison to these specialist dietary strategies, omnivores readily switch
76 between plants and animals depending on availability, and therefore face fewer constraints¹¹.
77 Still, the relatively high energy requirements of omnivores means that they must be selective
78 about the nutritional quality of their food—often focusing on smaller but denser diet items, such
79 as seeds, nuts, and insects¹². Given the universality of these shared constraints irrespective of
80 taxa or geography, we expect a consistent U-shaped trophic-size structure across taxonomic,
81 biogeographic, and temporal scales within vertebrates.

82 Here, we test the universality of this U-shaped trophic-size structure among vertebrates in
83 the present and, for terrestrial mammals, the consistency across deep time and towards future
84 centuries. We start by examining the robustness of the relationship across extant vertebrate
85 species with available data (5,033 mammals, 8,991 birds, 7,356 reptiles, and 2,795 fishes). We
86 also test whether the abiotic environment interacts with the U-shape as environmental conditions
87 are known to constrain body size (e.g., Bergmann’s rule¹³), by examining trophic-size structure
88 within and across all global biomes. For the evolutionary past, we investigate the emergence of
89 this trophic-size structure from fossil mammal records (5,427 species; Early Cretaceous to
90 Present). Finally, we examine the future of the U-shape structure by simulating projected
91 mammalian extinctions to determine if recent human-driven changes in extinction bias have the
92 potential to disrupt the existing trophic-size structure.

93 **Results**

94 Taxonomic universality

95 In terrestrial mammals, we find that herbivores and carnivores do indeed converge on the
96 largest body sizes (for both median and maximum values), while omnivores and invertivores are
97 limited to much smaller sizes, confirming the roughly U-shaped trophic-size structure described
98 previously (Fig. 2A; also see ⁴). Furthermore, we find that this trophic-size structure is nearly
99 universal among other modern vertebrate consumers, including terrestrial birds, reptiles, and
100 marine fishes (Fig. 2C, E, F). The convergence towards this trophic-size structure suggests that
101 its development and generality are robust to the highly variable life histories and evolutionary
102 trajectories of these groups. Even so, we find deviation from this structure in marine birds and
103 marine mammals (Fig. 2B, D), likely due to the additional body size constraints that are imposed
104 on vertebrates that have evolved secondarily aquatic lifestyles (e.g., thermoregulation and lung
105 capacity; see ^{14,15}). Moreover, invertivores in marine groups often achieve much larger sizes due
106 to the exploitation of unique filter feeding opportunities (e.g., bulk plankton feeding) and the fact
107 that the water medium can support much larger weights, making them non-analogous to the
108 terrestrial invertivore guilds¹⁶.

109 Biogeographic universality

110 When we break down the general patterns by individual biomes, we still consistently find
111 the U-shaped trophic-size structure for extant terrestrial mammals (Fig. 3), birds (Extended Data
112 Fig. 1), and marine fishes (Extended Data Fig. 2), despite the varying ecological and
113 evolutionary histories, degrees and types of disturbance and stability, climate, habitat structure,
114 and available energy for these systems and discrepancies between the dominant taxa. Minor
115 deviations from this trend are evident for the tundra and taiga biomes (herbivore median size is

116 lower than that of omnivores) and the temperate grassland biome (herbivore-omnivore non-
117 significant; further details in the Discussion). Still, changes in the relative frequencies of species
118 per guild across biomes do not appear to generally impact this relationship (Fig. 3). Thus, the
119 near-universality of trophic-size structure across biomes, particularly in terrestrial mammals,
120 suggests that it is fundamental to the structure and ultimately functioning of communities across
121 the planet.

122 Temporal universality

123 When we extend our analysis in terrestrial mammals over geologic timescales, we find
124 that the U-shape developed before the Paleocene Epoch (and potentially as early as the Early
125 Cretaceous, 145 Ma – 100.5 Ma) and has persisted for at least the last 66 million years (Fig. 4;
126 see also Extended Data Figs. 3-5). Therefore, the development of this trophic-size structure
127 seems to have preceded the establishment of mammals as the dominant terrestrial fauna
128 following the end-Cretaceous mass extinction 66 million years ago, when the largest land
129 animals until then, the dinosaurs, disappeared¹⁷. Terrestrial mammals reflect this trophic-size
130 structure in the majority of epochs since then (exceptions: herbivore median size lower than that
131 of omnivores in Oligocene; non-significant trophic-structure during Pliocene; see Discussion for
132 further details).

133 Effects of projected extinctions

134 The U-shaped trophic-size structure has been a feature of terrestrial mammals for
135 millions of years. Yet, we also reveal major disruptions to trophic-size structure. For instance,
136 the median and range of body sizes for herbivores and omnivores (~100 fold), and median body
137 size for carnivores (~10 fold), have generally decreased through the Pleistocene and Holocene in
138 parallel with the rise of early humans (Fig. 4), demonstrating a potentially important role for

139 human exploitation and other impacts in altering trophic-size structure¹⁸. Into the future, we
140 expect continued disruption, and indeed extinction simulations suggest that many large- and
141 medium-sized herbivores are likely to be lost, especially within the next 100-200 years (Fig. 5).
142 These future predicted extinctions (based on current IUCN extinction categorizations) suggest a
143 continued and rapid reduction in herbivore median and maximum body size over the next
144 century further disrupting the U-shaped relationship (Fig. 5). This reduction in mammal body
145 sizes may be at rates even greater than those experienced during the Pleistocene and Holocene
146 extinction events for all trophic guilds and for most continents (see Extended Data Fig. 6).

147 **Discussion**

148 Taken together, these taxonomic, biogeographic, and temporal patterns demonstrate that
149 a combination of evolutionary, physiological, and ecological pressures have driven a similar
150 trophic-size structure across nearly all modern vertebrates (Fig. 1 and Extended Data Table 1).
151 While the average and maximum body sizes of terrestrial mammals have indeed increased over
152 the Cenozoic¹⁹⁻²¹, this structure appears to have manifested during the Cretaceous (Fig. 4),
153 before the rapid diversification of mammals that followed the extinction of non-avian
154 dinosaurs^{22,23}. The fact that the different trophic guilds consistently maintained their relative
155 body size relationships to one another even when mammals were limited to smaller sizes during
156 the reign of dinosaurs suggests that evolutionary and physiological pressures (Fig. 1) alone
157 cannot explain this pattern. Further, the consistency of this pattern across biomes in multiple
158 classes of modern vertebrates (Fig. 3; Extended Data Figs. 1 and 2) suggests that ecological
159 assembly processes and the distribution of niches within local areas play an important role in
160 maintaining this pattern.

161 Although trophic-size structure is consistent across vertebrates, biomes, and epochs, we
162 identify some notable deviations. For instance, secondarily marine mammals and birds do not
163 exhibit the same structure. This can be explained by a combination of strong physiological
164 constraints imposed on “warm blooded” species living in the oceans (e.g., limited capacity to
165 buffer body temperature), the relaxation of the maximum body size due to living in the aquatic
166 medium (e.g., because mass is displaced by water), and the exploitation of unique filter feeding
167 opportunities where high-quality food is available in large quantities^{14,15,24,25}. In addition,
168 omnivorous mammals in the cold and dry tundra and taiga biomes tend to be larger than
169 omnivores in other biomes, although this difference is not statistically significant (see
170 Supplementary Table 1). This is likely due to the seasonality of high-quality plant sources which
171 constrain omnivores to diets consisting of low-quality plants or vertebrates for much of the
172 year^{26,27}, tipping them towards strategies that characterize large herbivores and carnivores. The
173 species trophic guild assignments in our database are coded at the global scale, so they might not
174 account for dietary differences or prey switching such as this at the biome level. Therefore, it is
175 also possible that these species are entirely or nearly entirely herbivorous or carnivorous in these
176 biomes, and, if so, this would explain why they exhibit similar sizes to these other trophic guilds.
177 Further, it is also possible that the small sample sizes of omnivorous species in these biomes
178 (tundra: 7, taiga: 15) might be leading to less accurate results than would be derived from larger
179 sample sizes. Temperate grasslands also show no clear difference between herbivores and
180 omnivores. We attribute this to the loss of many large herbivores across this biome during the
181 late Pleistocene extinctions (e.g., several species of mammoth, bison, and horses)^{28,29}. Finally,
182 the average invertebrate size varies significantly between some biomes (21 of 91 pairwise
183 comparisons, see Supplementary Table 1). Eight of these 21 comparisons include the tundra
184 biome, indicating that invertebrate diets in the tundra potentially cannot sustain sizes as large as

185 those in other biomes. For the remainder of these comparisons, we propose that the narrow
186 distribution of invertivore body sizes combined with large sample sizes may be leading to
187 spurious Mann-Whitney *U*-test results. Outside of these differences among invertivores, the
188 distributions (medians and 90th quantiles) of mammal body sizes within trophic guilds are similar
189 between biomes (Supplementary Tables 1 and 2).

190 While the different trophic guilds have similar distributions during the Cretaceous period,
191 some of their 90th quantiles are statistically different. With larger sample sizes during this period,
192 we expect the differences in medians would become statistically significant. During the
193 Oligocene, omnivores exhibit larger average sizes than herbivores (although not significantly).
194 These results may be related to climatic cooling³⁰ during this time period, although fossil
195 preservation and sampling biases can lead to unexpected results when examining patterns within
196 the fossil record (see Methods; Extended Data Figs. 3-5). However, rather than cause the
197 consistent trophic-size structure we observe, fossil preservation biases are most likely to
198 introduce noise, including through time averaging³¹, and obscure ecological signals (see
199 Methods). Despite this and other minor deviations, we see statistically different 90th quantiles
200 between herbivores and omnivores and between carnivores and insectivores across the entire
201 Cenozoic (66 Ma to present), indicating the U-shape is persistent across this era.

202 Recent and projected future extinctions (Fig. 5) indicate that this longstanding near-
203 universal U-shaped structure may be disrupted by anthropogenic activities. Past downsizing of
204 terrestrial herbivores – driven by the extinction of larger species – has previously altered
205 ecosystems by reducing seed dispersal distances, modifying fire regimes, and transforming
206 vegetation structure³²⁻³⁴. These ecosystem changes could be exacerbated in the future through
207 predicted extinctions of many of the remaining larger herbivores (Fig. 5), and such extinctions
208 may also result in other negative ecosystem changes. For example, large-bodied herbivores

209 exploit large amounts of resources over broad scales, leading to important contributions to
210 nutrient transfer over vast distances³⁵. The extinction of these herbivores will likely result in
211 reduced energy transfer (and thus reduced ecosystem productivity), degraded ecological
212 interactions, and reduced ecosystem resilience to climate change^{35,36}. Similar changes are
213 expected to occur in the marine realm due to the loss of marine herbivores, such as a reduction in
214 the capacity of large fishes to control algal overgrowth and to produce carbonate sediments on
215 coral reefs^{37,38}.

216 At the same time, the introduction and increase in vertebrate livestock (most of which are
217 herbivores) across the globe, in both agricultural and wilderness areas, could further exacerbate
218 these changes through associated overgrazing and indirect effects, such as eutrophication,
219 erosion, and increased carbon emissions³⁹. Other management actions, such as fencing, may also
220 introduce barriers to dispersal, which will likely alter the biome-level patterns documented
221 here⁴⁰. Moreover, livestock are protected (e.g., from disease) by and support humans
222 (omnivores) and thus represent a collapsed food web and focused energy transfer.

223 The projected loss of wild herbivores (Fig. 5) also has the potential to trigger co-
224 extinctions of large carnivores which depend on lower trophic levels to meet their nutritional
225 needs^{41,42}. These potential co-extinctions are not directly accounted for in our extinction forecast
226 (i.e., the IUCN Red List does not directly incorporate prey abundance), and could further disrupt
227 trophic-size structure and compromise ecosystem functioning⁴³. Furthermore, the effects of
228 downsizing and co-extinctions could be amplified by possible impacts of future climate change
229 on body size that have also been hypothesized to lead to smaller body mass in mammals (e.g.,⁴⁴)
230 and ectotherms⁴⁵.

231 The predicted future decline and extinction of wild mammals described here, which is
232 likely underestimated by not including co-extinctions, could generate strong ecological and
233 trophic consequences for wilderness areas, comparable to those triggered by past megafaunal
234 extinctions^{18,46-49}. Moreover, these changes are currently being seen in marine environments,
235 such as the loss of otters in Pacific kelp ecosystems^{37,50}. Thus, fundamental ecological assembly
236 rules that have been in operation since before the beginning of the age of mammals are likely to
237 be disrupted. While we have not examined the same future trajectories for phyla other than
238 mammals due to data limitations, we know that similar extinctions are expected for marine
239 fishes, reptiles, and birds due to global change drivers such as habitat loss, over-exploitation,
240 disease, and climate change⁵¹. Thus, we surmise that the shared U-shaped trophic-size structure
241 exhibited by these groups (Fig. 1) is also likely to continue to be disrupted in the coming
242 decades, leading to a dramatic global shift in Earth's ecosystem processes not seen in at least 66
243 million years.

244

245 **Methods**

246 In brief, we summarized trophic-size structure for mammals through time, with body mass
247 comparisons across four trophic guilds (herbivores, omnivores, invertivores, and carnivores). We
248 assessed the consistency of emergent patterns across biomes and also taxa. We compared the rate
249 of extinction in the different trophic guilds through the past and future. We used R version
250 4.1.0⁵² for all our analyses. See R code summarizing the major analytical steps
251 (<https://github.com/willgearty/Trophic-Extremes>).

252 Consistency of U-shape across taxa

253 To evaluate the consistency of the U-shape across vertebrate consumers, and across
254 endothermic and ectothermic animals from both marine and terrestrial realms, we undertook
255 global analyses of trophic-size structure for mammals (terrestrial), marine mammals, birds
256 (terrestrial), marine birds, reptiles, and fishes (Fig. 2) (see below for data sources). We analyzed
257 marine birds and marine mammals separately from their terrestrial relatives due to the different
258 energetic constraints across marine and terrestrial realms^{14,15}. We defined marine birds as those
259 birds that feed at sea, either nearshore or offshore⁵³ - families: Alcidae, Anhingidae,
260 Diomedidae, Fregatidae, Gaviidae, Hydrobatidae, Laridae, Oceanitidae, Pelecanidae,
261 Phaethontidae, Phalacrocoracidae, Podicipedidae, Procellariidae, Spheniscidae, Stercorariidae,
262 and Sulidae. We defined marine mammals as those mammals that generally inhabit marine
263 and/or freshwater systems - families: Balaenidae, Balaenopteridae, Cetotheriidae, Delphinidae,
264 Dugongidae, Eschrichtiidae, Iniidae, Kogiidae, Lipotidae, Monodontidae, Odobenidae,
265 Otariidae, Phocidae, Phocoenidae, Platanistidae, Pontoporiidae, Trichechidae, and Ziphiidae.

266 We used the best available diet and body size data for each taxonomic group (we only
267 included species with complete diet and body size data): mammals (terrestrial) (5,033 species;
268 using a previously collated database⁵⁴ - primarily derived from four datasets⁵⁵⁻⁵⁸), marine

269 mammals (118 species⁵⁵⁻⁵⁸), birds (terrestrial) (8,991 species⁵⁴), marine birds (281 species⁵⁴),
270 reptiles (7,356 species⁵⁹), and fishes (2,795 species⁶⁰). For fishes, estimates of body mass are
271 scarce, so we used maximum body length, which is a more commonly measured value of body
272 size for fish and is known to scale predictably with size. We classified species into four trophic
273 guilds based on diet proportions where available (mammals and birds⁵⁷): herbivores (>50% use
274 of plants, including plant material, fruits, nectar and seeds), invertivores (>50% use of
275 invertebrates), carnivores (>50% use of vertebrates, including endotherms, ectotherms, fish and
276 carrion), and omnivores (\leq 50% use of plants, invertebrates and vertebrates). We translated the
277 reported diet data for reptiles to match the trophic guilds for mammals and birds, however this
278 was not possible for fishes.

279 Our trophic guild classification and trophic guild order (e.g., herbivore - omnivore -
280 invertivore - carnivore) were selected to characterize a gradient from plant-based diets to animal-
281 based diets. This plant-animal gradient represents a transition between high carbohydrate dietary
282 materials to high protein dietary materials³, and hence reflects changes in dietary nutritional
283 content⁵. In addition, the gradient reflects a general shift in trophic level from primary consumers
284 (i.e., herbivores) to secondary, tertiary, etc. consumers. This shift in trophic level underpins the
285 separation of invertivores from carnivores. While these two guilds have been combined in other
286 work², this ignores the fact that they have differing average trophic levels, differing ecological
287 roles, and differing ecophysiological body-size constraints (¹⁶; Fig. 1 and Extended Data Table
288 1). Here we use a coarse trophic guild classification, which will inevitably lose some of the finer
289 dietary specialization between species⁶¹, but allows us to analyze broad patterns in the
290 relationship between body mass and diet across vertebrates². Overall, our trophic guild
291 classification and guild order reflects diet nutritional content and the average trophic level of

292 consumers, captures major ecological differences between species, and is underpinned by
293 multiple ecophysiological constraints (Fig. 1 and Extended Data Table 1).

294 We used Mann-Whitney *U*-tests to assess whether pairwise trophic guilds had statistically
295 different body size distributions. We used non-parametric permutation tests to assess whether the
296 90th quantiles of the body size distributions of pairwise trophic guilds are statistically different.
297 We performed 5,000 random permutations to establish a null distribution of 90th quantile
298 differences, then compared the observed 90th quantile difference to estimate the probability (p-
299 value) that this difference occurred due to random chance. The p-values from these two sets of
300 tests have been corrected for multiple tests within each taxonomic group ($n = 3$) using the Holm
301 method⁶² and are displayed in Fig. 1.

302 Consistency of U-shape across biomes

303 To test for spatial (biogeographic) consistency in the U-shape across biomes with markedly
304 different environmental characteristics we analyzed extant terrestrial mammal (Fig. 3) and extant
305 terrestrial bird (Extended Data Fig. 1) species pools for each terrestrial biome⁶³, and extant fish
306 (Extended Data Fig. 2) species pools for each marine biome (⁶⁴; although not strictly equivalent,
307 for simplicity, we treat the realms of ⁶⁴ as marine biomes). We assigned mammals and birds to
308 all global terrestrial biomes⁶³ in which they occur based on their geographic distributions (only
309 including areas in which the species is native or reintroduced) obtained from the IUCN
310 (<https://www.iucnredlist.org/resources/spatial-data-download>). We assigned fishes to global
311 marine biomes⁶⁴ in which they were surveyed⁶⁰. We performed Mann-Whitney *U* and 90th
312 quantile permutation tests as described above. The resulting p-values were corrected for the
313 number of pairwise tests across all biomes ($n = 42$). We also performed similar tests to compare
314 the distributions of mammal body sizes within individual trophic guilds between different
315 biomes (Supplementary Tables 1 and 2). For the permutation tests, we performed 100,000

316 replicates. The number of replicates was increased in this case (compared to the 5,000 described
317 above) to increase the power of the test after correcting for the large number of pairwise tests
318 performed ($n = 364$). The resulting p-values were corrected for the total number of pairwise tests
319 performed ($n = 364$).

320 Consistency of U-shape across time

321 For the temporal analysis, we used body mass and fossil range data previously compiled for
322 5,236 mammals since the Cretaceous^{19,21}. Within this dataset, mammals are classified into one of
323 four trophic guilds: herbivores (primarily a browser or grazer), omnivores (ambiguous or mixed
324 diet), invertivores (exclusively eat invertebrates), and carnivores (primarily eating meat,
325 excluding insects and earthworms). We supplemented this data by obtaining body size estimates
326 for 191 additional mammals using osteological measurements and allometric equations from the
327 primary literature (see Supplementary Tables 3 and 4 for details). Diets for all mammals were
328 based on expert opinions in the Paleobiology Database using the trophic guild classification
329 scheme outline above. Fossil ranges for these mammals were also obtained from the
330 Paleobiology Database assuming the oldest possible origination and the youngest possible
331 extinction. We used the first and last fossil appearances of each mammal to code their presence
332 or absence in each epoch from the Early Cretaceous to the Holocene (Fig. 4; see Supplementary
333 Table 5). We performed Mann-Whitney U and 90th quantile permutation tests as described above
334 within each epoch. The resulting p-values were corrected for the number of pairwise tests across
335 all epochs ($n = 27$).

336 For each trophic guild within each epoch that had at least five species we performed a
337 bootstrapping approach to assess uncertainty in their body mass distributions. We performed
338 1,000 bootstraps and calculated means and standard deviations for each bootstrap replicate. The
339 distributions of the means are reported in Extended Data Fig. 3 and weighted means and standard

340 deviations are reported in Extended Data Fig. 4. Finally, we performed a subsampling approach
341 where we took random samples of increasing size from each trophic guild within each epoch. We
342 repeated this 100 times, and then we calculated the mean and standard deviation for each sample
343 (Extended Data Fig. 5).

344 Potential effects of biases in fossil data

345 We considered potential biases in the fossil record and how they might affect
346 documented patterns and our interpretation of those patterns. For the purposes of the analyses
347 included here, the main issue is the bias against preservation of small-bodied species⁶⁵. However,
348 live-dead studies have shown that the ecological structure of mammalian communities are
349 retained in death assemblages⁶⁶ suggesting that ecological signal is recoverable from fossil data.
350 Regardless, if there were to be such a bias against smaller-sized species in our sampling,
351 invertivores would be preferentially impacted as they tend to be small-bodied (Fig. 2, see ⁶⁷).
352 However, even with this potential bias, invertivores are consistently (and statistically) the
353 smallest trophic guild through time (Fig. 4) and would possibly be even smaller on average
354 without this preservation bias. Also, we did not exclude species below a certain size as that
355 would have differentially biased our estimates of the body size distributions of the different
356 trophic guilds as they do not encompass the same body size ranges. Bootstrap and subsetting
357 analyses indicate that the identified patterns are robust (Extended Data Figs. 3-5). Moreover,
358 they suggest that deviations from the overall U-shape in the Oligocene are not statistically
359 significant and may be a result of a low omnivore sample size during this epoch. Importantly,
360 these biases in fossil data should introduce noise into these patterns and are unlikely to cause a
361 U-shaped pattern in body size among trophic guilds.

362 Consistency of U-shape in the future

363 We simulated yearly future extinction scenarios for 4,804 terrestrial mammal species (those
364 with data available for diet, body mass, generation length⁵⁶ and IUCN status) over a 500 year
365 time horizon using the iucn_sim program, version 2.1.1⁶⁸; 10,000 extinction simulations. The
366 iucn_sim program uses extinction probabilities derived from the IUCN Red List⁶⁹ (e.g., Least
367 Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct/Extinct in
368 the Wild) to simulate future extinctions⁶⁸. Specifically, the history of the Red List (i.e., historic
369 status changes and the cumulative amount of time spent in each status) is used to inform
370 potential status transitions away from a species' current status (e.g., transitions from Critically
371 Endangered to Extinct, or Endangered to Vulnerable) through time⁶⁸. Historic status changes are
372 therefore assumed to characterize the potential for future status changes. Species' generation
373 lengths are used to adjust the time frame associated with the transitions⁶⁸. The simulations can
374 then be used to estimate extinction probabilities, based on transitions to the Extinct status. For
375 further details of the extinction models see ⁶⁸.

376 We quantified body mass trajectories using the diet and body mass data for extant terrestrial
377 mammals⁵⁴ and the estimated extinction dates generated by iucn_sim⁶⁸. We calculated the mean
378 and 95% confidence interval (i.e., the 2.5th and 97.5th percentiles) across the 10,000 simulations
379 of median log mass per trophic guild per year. The median extinction probabilities across all
380 extant mammals are reported in Supplementary Table 6.

381 Comparison of U-shape future changes to Pleistocene changes

382 We calculated the median body size for each continent before and after the Pleistocene
383 extinctions based on mammal body sizes in the updated MOM database²¹. We then calculated
384 the median body size for each continent before and after the predicted future extinctions based
385 on extant species (before) and extant species minus species identified as threatened on the IUCN
386 red list (after), again using the MOM database²¹. The lengths of the continent-specific

387 Pleistocene extinctions were estimated based on the timing of the major extinctions reported in⁷⁰
388 (which is based on²⁹). The lengths of the predicted future extinctions are set to 500 years to
389 correspond to the projections in Fig. 5. Rates were calculated as the changes in median body size
390 across the extinctions divided by the lengths of the extinctions (Extended Data Fig. 6).

391

392 **Data availability**

393 All data are available at <https://github.com/willgearty/Trophic-Extremes>.

394

395 **Code availability**

396 All code is available at <https://github.com/willgearty/Trophic-Extremes>.

397

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411 Tennenbaum Marine Observatories Network. This is Paleobiology Database publication 420.

412

413 **Author contributions**

414 RC, WG, ASAC, JD, GJE, JSL, GR, CRM, RDS-S, SKL, and AEB conceived of the project.

415 RC, WG, SKL, AEB, GJE, RDS-S, GR, and JSL contributed data. RC, WG, SKL, and AEB

416 developed the methodology and performed statistical analyses. RC and WG created the

417 visualizations. ASAC and AEB acquired funding for the project. SKL and AEB jointly

418 supervised the project. RC and WG wrote the original draft of the manuscript. RC, WG, ASAC,

419 JD, GJE, JSL, GR, CRM, RDS-S, SKL, and AEB helped revise the manuscript.

420

421 **Competing interest declaration**

422 Authors declare that they have no competing interests.

423 **Additional Information**

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427

Trophic Guild	Type of Constraint	Mechanism	References
Herbivores	Minimum Size	Physiology: Need to be big enough to have digestive systems efficient (large) enough to extract enough energy; smallest herbivores are eating fruit or seeds which are energy dense	8
	Promotes Smaller Size	High quality plant resources (fruit/seeds) are lower in abundance and seasonal	5
		Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Jarman-Bell principle (larger species can survive on lower quality forage)	6,7
		Able to travel farther (and migrate)	72
		Large size is a generally effective strategy for protection against predators	33
	Maximum Size	Lower quality resource availability	12
		Biomechanical (bone density/structure, heart size/circulation, overheating)	73,74
		Plant fermentation efficiency limit	72
Omnivores	Minimum Size	Physiology: High mass-specific metabolism, need very high protein food source	11
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	Resource availability: Larger than max size of carnivores (e.g., bears) because they can rely on plants when animals are unavailable; smaller than max size of herbivores because they lack the digestive systems required to process bulk energy-poor foods	12
Invertivores	Minimum Size	Physiology: High mass-specific metabolism, need very high protein food source	11
		Need to be larger than their prey	9
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	For terrestrial mammalian invertivores, the abundance, distribution and energy content of terrestrial invertebrates are not sufficient to support body masses above 20 kg	10
Carnivores	Minimum Size	Need to be larger than their prey (at least at these sizes)	9
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Patchiness of food favors fasting and starvation resistance afforded by larger sizes	75
		Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	1,100 kg limit due to tradeoff of high hunting costs versus payoff	10

429 **Extended Data Table 1. Theoretical mechanisms of body size constraints in vertebrates by**
 430 **trophic guild from the primary literature.**

431

432 **Figure Legends**

433 **Fig. 1. Observed limits and conceptual mechanisms relating body size to trophic guild**
434 **across the world's terrestrial mammals.** White boxes indicate maximum body size when
435 including prehistoric and historic extinct species. Grey boxes indicate the potential maximum
436 body size decreases if all IUCN threatened (Vulnerable, Endangered, Critically Endangered)
437 species are lost. Mass limits (vertical bars) are based on data from Smith et al.²¹, while the
438 mechanisms (horizontal lines and associated labels) are conceptual and based on the literature
439 (see Extended Data Table 1 for further details). Silhouettes are from phylopic.org and represent
440 the smallest and largest species for each trophic guild.

441
442 **Fig. 2. Contemporary global trophic-size structure across taxa.** Body size distributions per
443 trophic guild for (A) 5,033 mammal (terrestrial) species, (B) 118 marine mammal species, (C)
444 8,991 bird (terrestrial) species, (D) 281 marine bird species, (E) 7,356 reptile species, and (F)
445 2,795 fish species. Trophic guilds are ordered following a gradient of plant-based to animal-
446 based diets and increasing average trophic level (see Methods); labels indicate the number of
447 species per trophic guild. Note that the (log) body size scale is taxonomic group specific. Stars
448 represent p-values from pairwise two-sided Mann-Whitney *U*-tests (black stars, at the bottom of
449 panels) and 90th quantile two-sided permutation tests (white stars, at the top of panels) after
450 correcting for multiple comparisons ($0 < *** < 0.001 < ** < 0.01 < * < 0.05$) and are located
451 between the test pairs (see Methods). Silhouettes are from phylopic.org and show example
452 species for each taxonomic group. Boxplot elements are as follows: center line, median; box
453 limits, upper and lower quartiles; whiskers, 1.5x interquartile range.

454

455 **Fig. 3. Trophic-size structure across global biomes for terrestrial mammals.** Body mass
456 distributions (log scale) per trophic guild for 5,033 terrestrial mammal species across biomes.
457 Mammals were assigned to all biomes in which they occur. Labels indicate the number of
458 species per trophic guild. Biomes are ordered by their absolute latitudinal distribution. Boxplot
459 elements and stars as in Fig. 2.

460

461 **Fig. 4. Trophic-size structure of 5,427 terrestrial mammal species through time.** Body mass
462 distributions (log scale) across trophic guilds for terrestrial mammals since the Early Cretaceous,
463 145 million years ago (Ma) (Supplementary Table 5). Colored numbers represent sample sizes
464 corresponding to trophic guilds. Silhouettes are from phylopic.org and show example species for
465 each time interval. Boxplot elements and stars as in Fig. 2.

466

467 **Fig. 5. Change in mass into the future.** Percent change in (A) the median and (B) the 90th
468 quantile of wild terrestrial mammal body mass per trophic guild predicted up to 500 years into
469 the future. The bold lines show the mean trajectory, and the envelopes show the 95% confidence
470 intervals per year across 10,000 simulations; the dashed lines show the present-day body mass
471 value (median or 90th quantile) for each trophic guild. (C) Illustration showing examples of large
472 terrestrial mammals lost during the Pleistocene (light shade), those that are forecast to be lost
473 into the future (medium shade; probability of extinction >50%), and those likely to persist (dark
474 shade; probability of extinction <20%) (see Supplementary Table 6). The smallest mammals of
475 each guild, magnified in the insets, show little change across these intervals.

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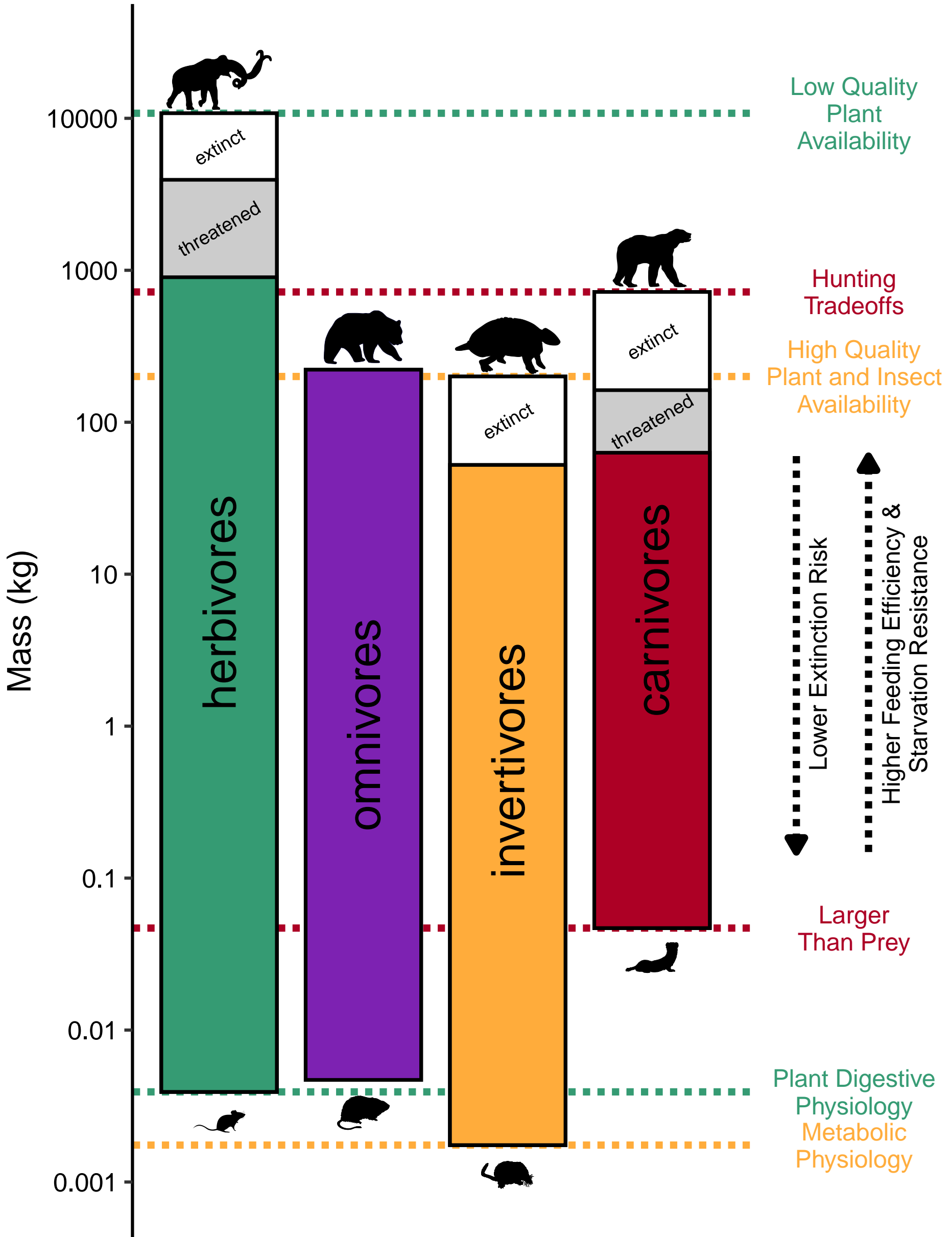
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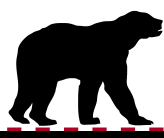
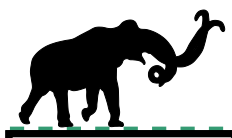
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Low Quality Plant Availability

Hunting Tradeoffs

High Quality Plant and Insect Availability

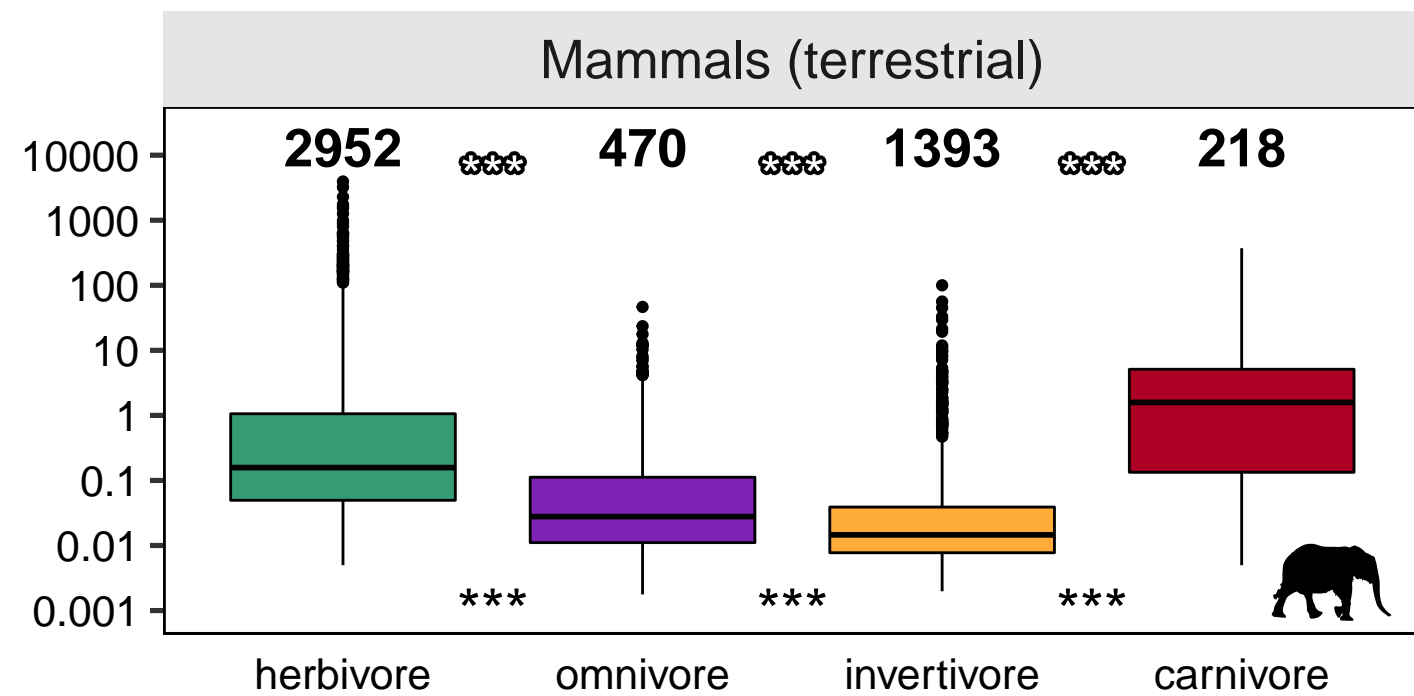
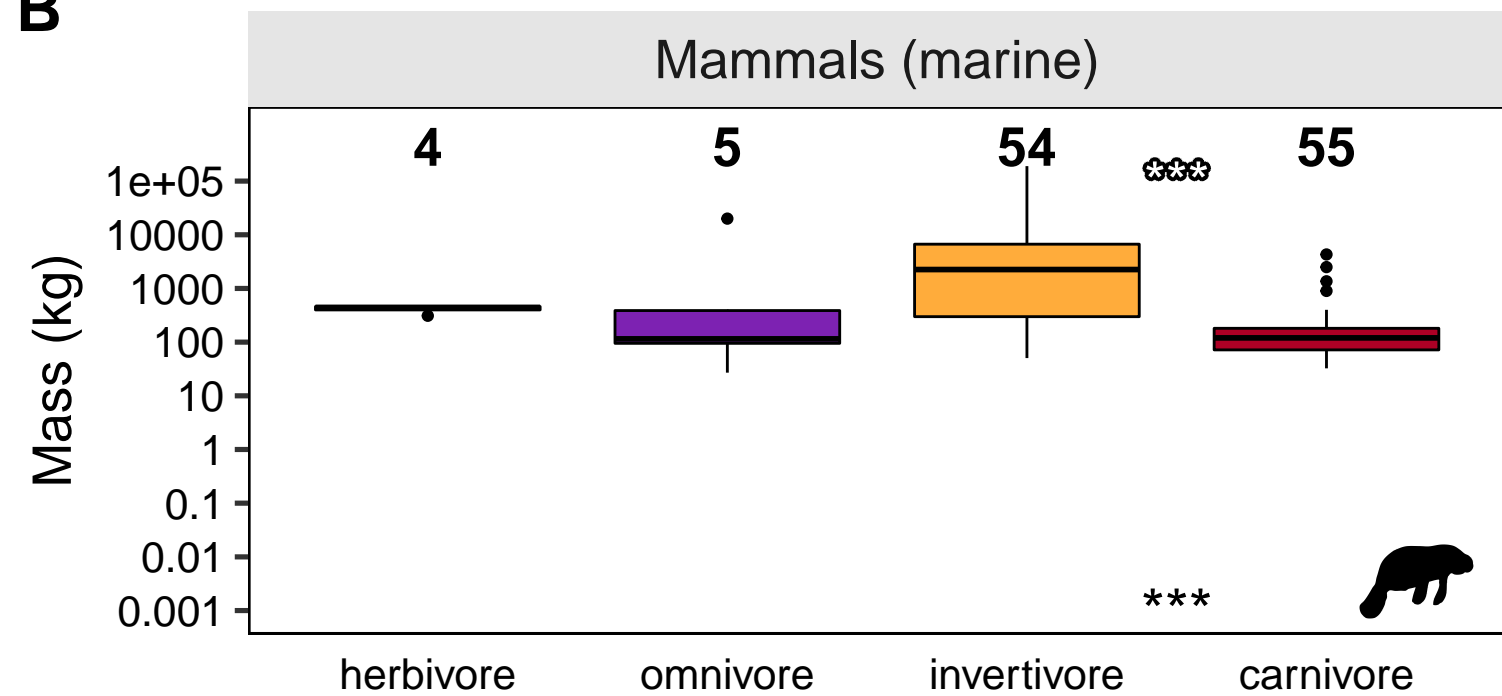
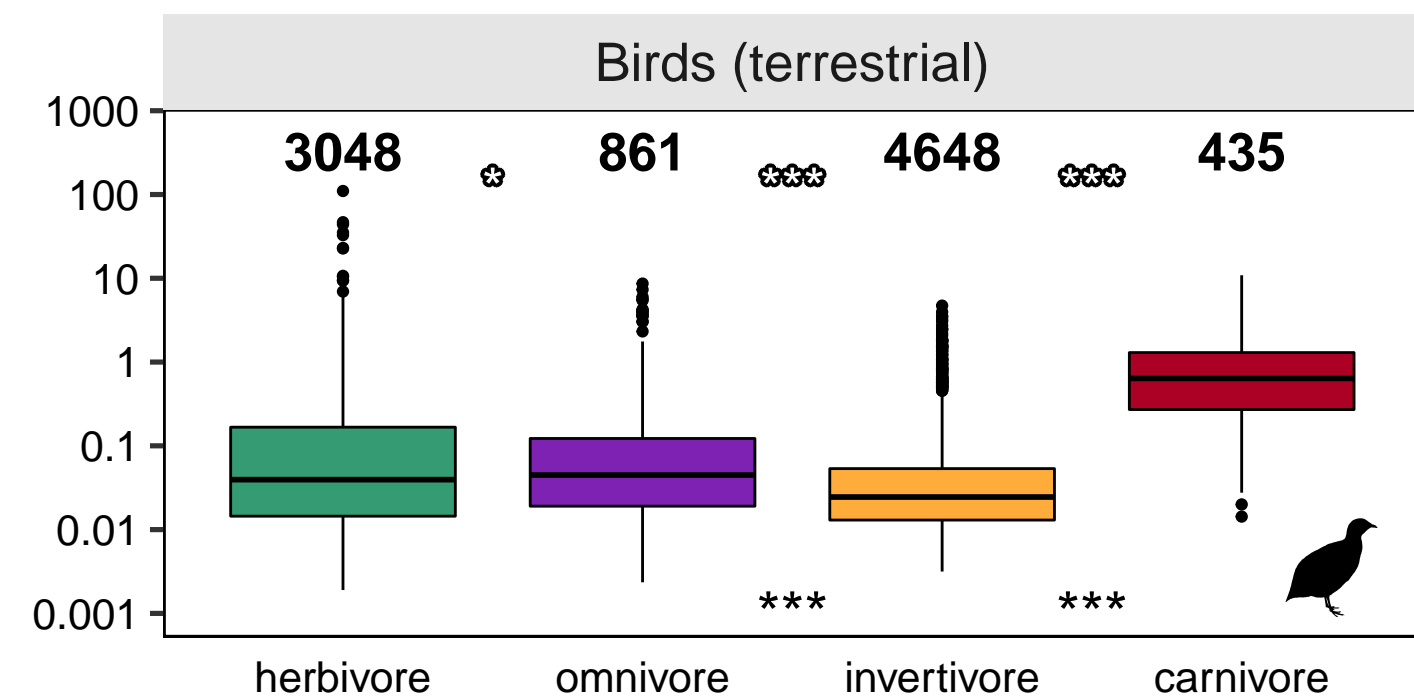
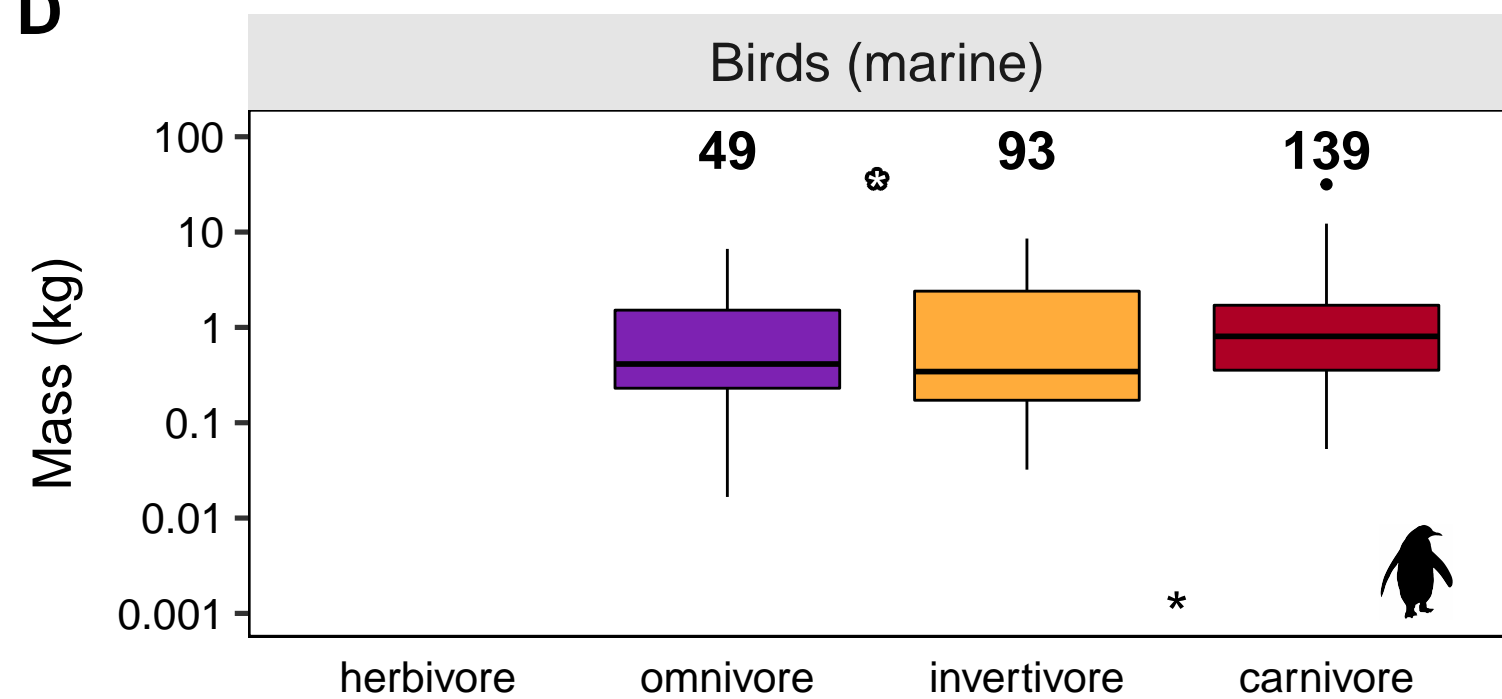
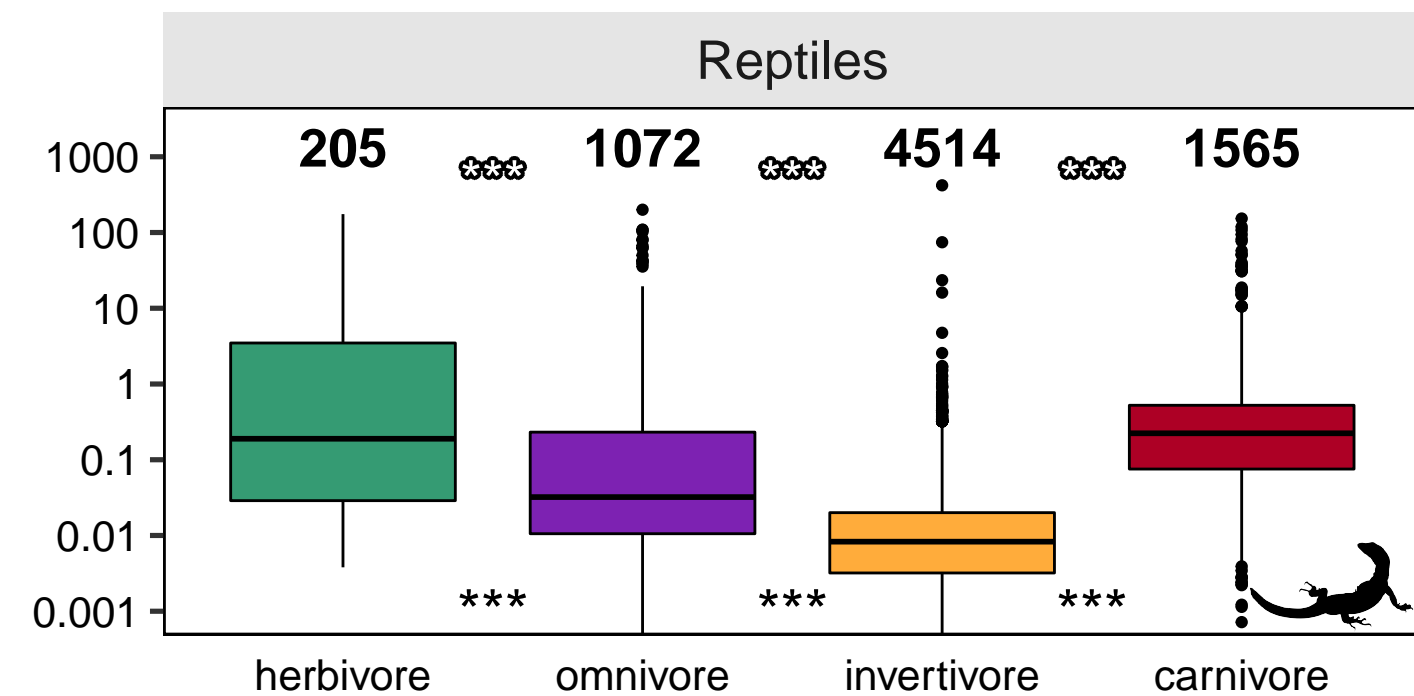
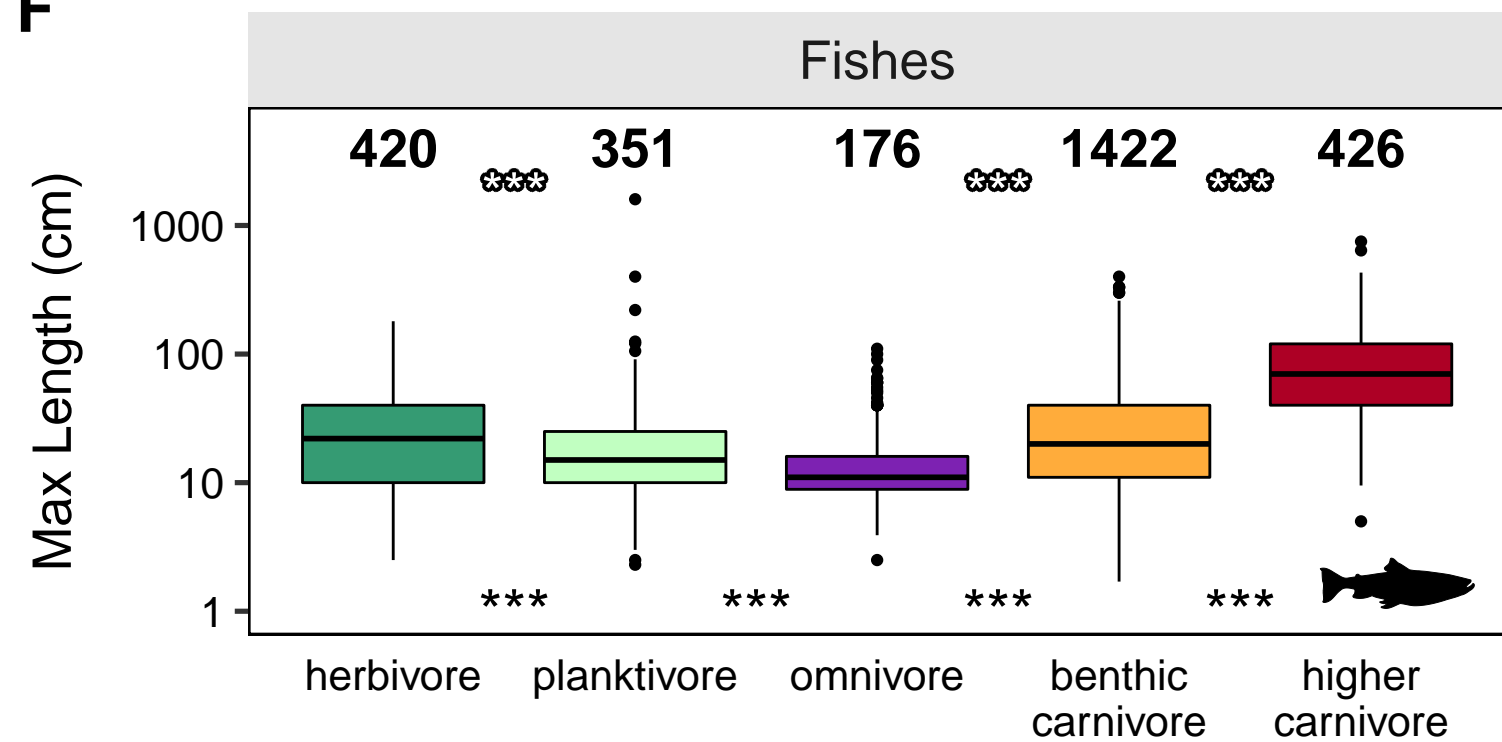
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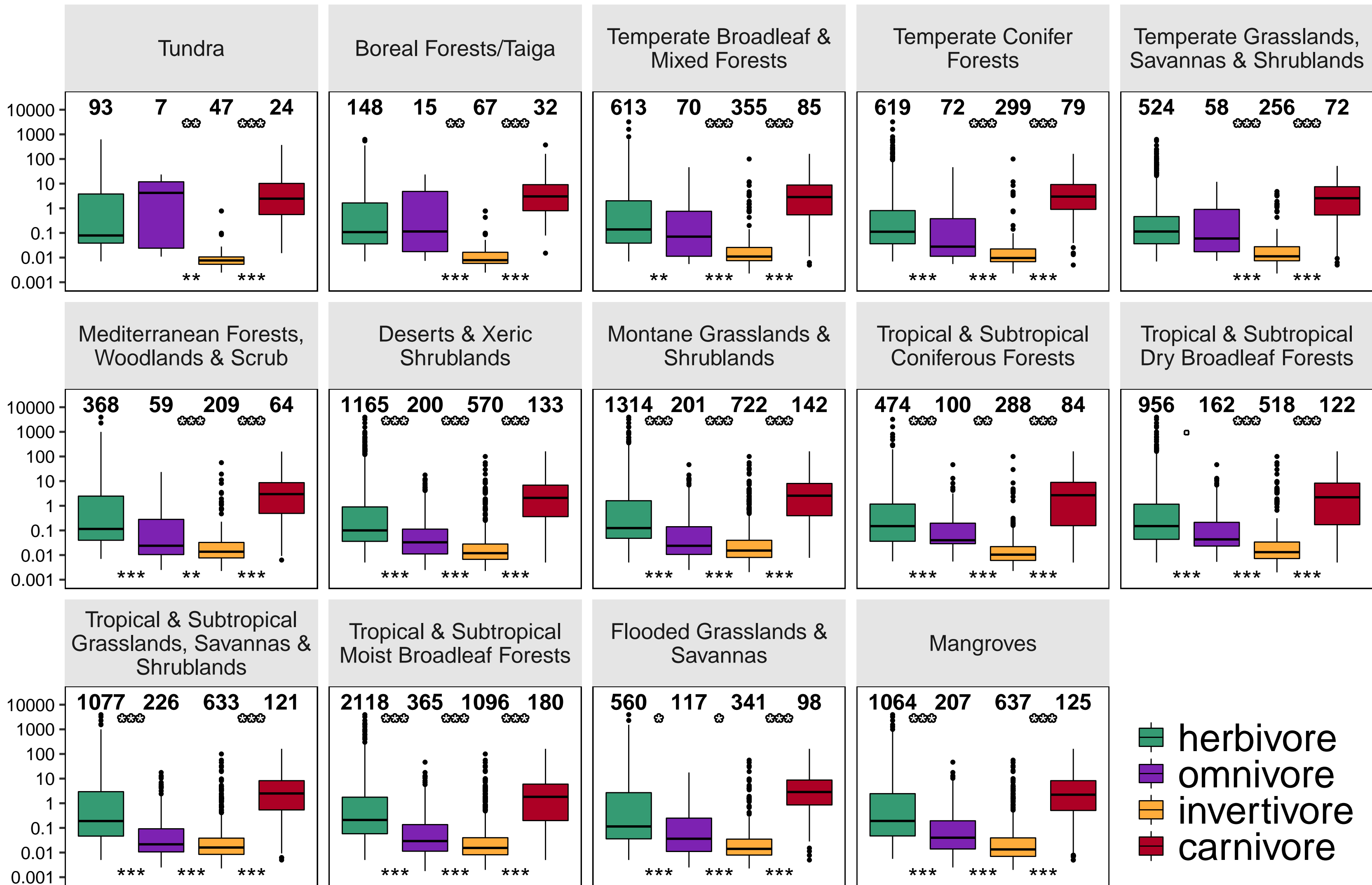
Higher Feeding Efficiency & Starvation Resistance

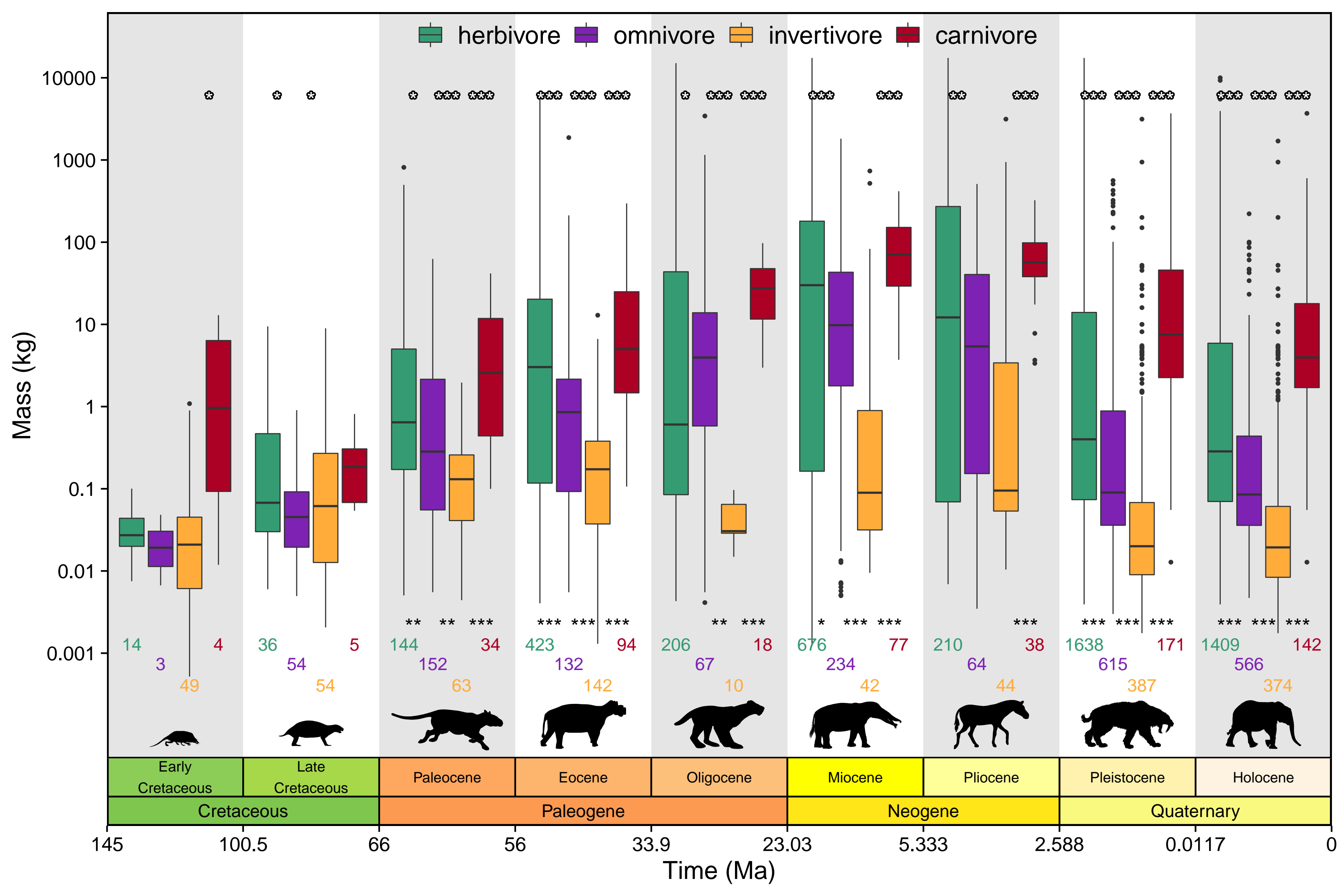
Larger Than Prey

Plant Digestive Physiology

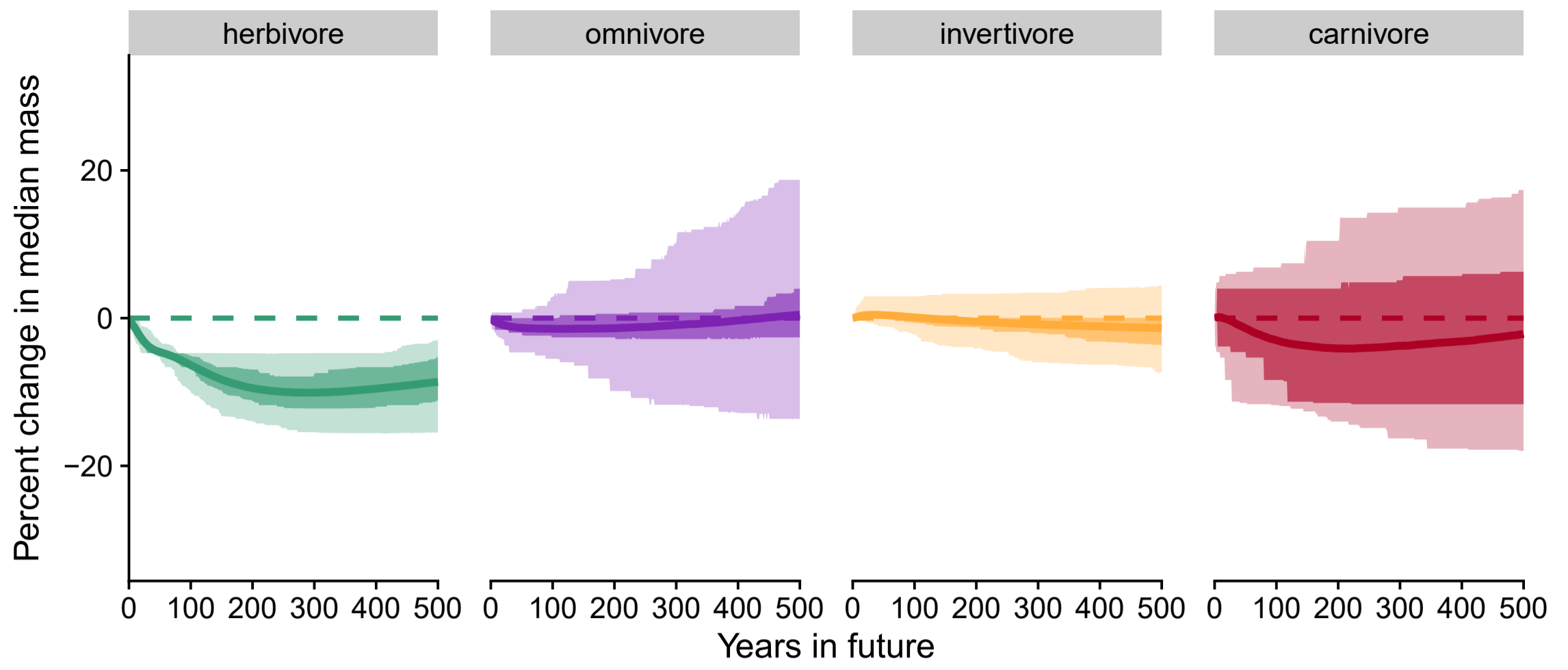
Metabolic Physiology

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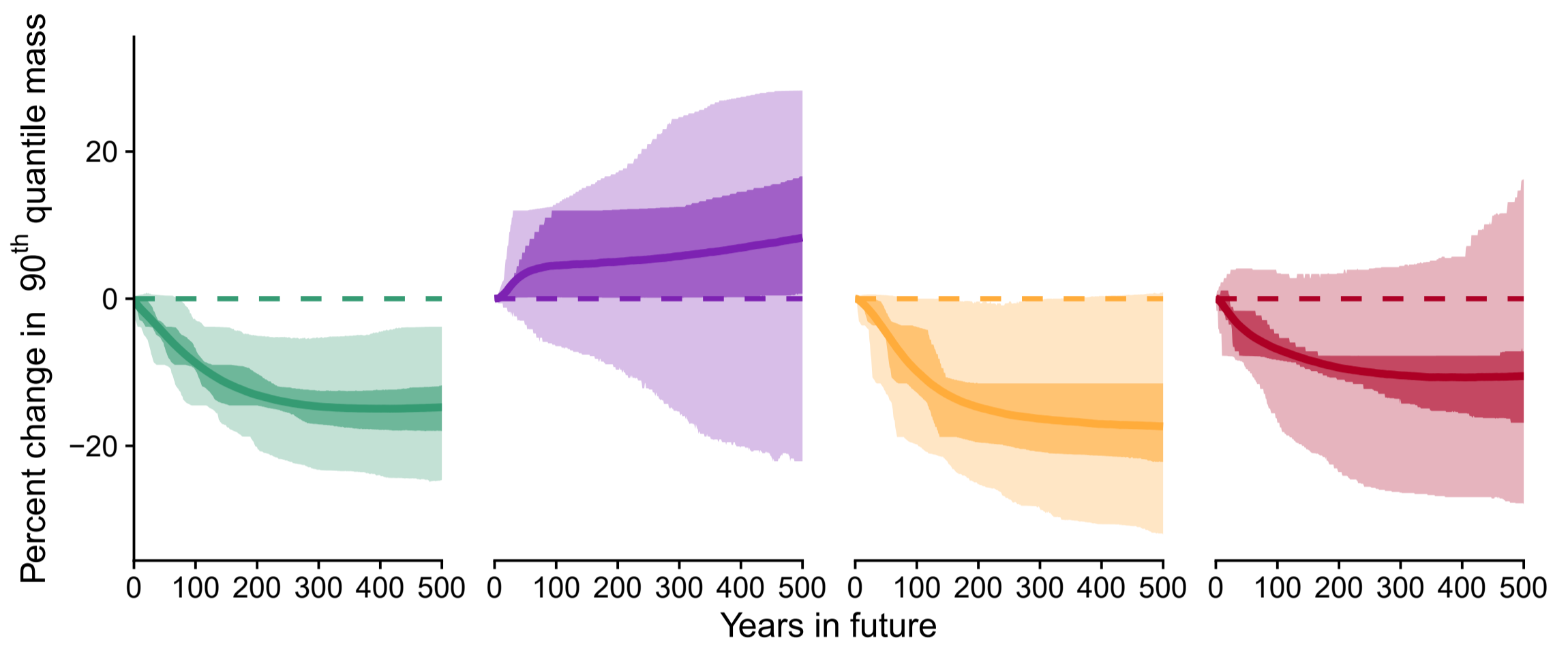




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